Eur J Forest Res (2011) 130:717–727
DOI 10.1007/s10342-010-0461-5

ORIGINAL PAPER

Cost-effective strategies to conserve boreal forest biodiversity and long-term landscape-level maintenance of habitats

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Received: 16 June 2010 / Revised: 19 October 2010 / Accepted: 25 November 2010 / Published online: 17 December 2010

Abstract Setting aside parcels of land is the main conservation strategy to reduce the rate of biodiversity loss worldwide. Because funding for biological conservation is limited, it is important to distinguish the most efficient ways to use it. Here, we assess implications of alternative measures to conserve biodiversity in managed boreal forest landscapes. We calculated four alternative spatio-temporal scenarios and compared these to the current management regime over 100-year time period. In the alternative scenarios, a fixed amount of funding was invested in (1) permanent large reserves (each tens of ha in size), (2) permanent small reserves (each a few ha in size), (3) temporary small reserves (based on 10-year contracts with private land owners), and (4) green-tree retention (small groups of trees retained on clear-cuts). To assess biodiversity implications, we used habitat suitability indices to calculate overall habitat availability for five groups of red-listed and habitat-specific species associated with decaying spruce logs. The possibilities for timber harvests did not differ among the scenarios, but biodiversity performance was different. The scenarios with permanent reserves tended to outperform other scenarios, suggesting that conservation policies based on permanent reserves are the most cost-efficient in the long term. Results, however, varied among time scales and species groups. In the short term, a strategy of investment in temporary small reserves was the most efficient. Habitat for species associated with old spruce dead-wood and preferring shade was rare throughout all simulations, and therefore, it is likely that these species cannot be sustained in managed forests. Species that live on fresh dead-wood and are associated with forest edges coped well in all scenarios suggesting that such species will persist in managed landscapes without additional conservation

Communicated by M. Moog.

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efforts. Explicit definition of conservation objectives and time frames for conservation action are thus prerequisites for successful conservation planning.

Keywords Boreal · Conservation planning · Dead-wood · Forest management · Habitat suitability · Red-listed species · SELES · Simulation

Introduction

Habitat loss is a globally recognized threat to biodiversity, and efficient tools are sought to halt undesirable trends of species loss. Further development of existing protected-area networks may contribute to a solution. Protected forest areas and managed forests are intermingled in all forest landscapes, and thus, maintenance of biodiversity depends on both (Polasky et al. 2005). All management practices in commercial forests affect the landscape where protected areas are embedded, but simultaneously, conservation actions also influence the management planning. Therefore, an integrated approach is needed to sustain forest biodiversity. Integrated approach is particularly relevant in European landscapes that have a long history of human influence and variety of protected areas.

There are several ways to achieve biodiversity conservation goals in a given region. If funding for conservation is limited, it is important to discern the best ways to allocate it. Among the alternatives that can be used to meet the objectives under given resource constraints, the one that provides maximal biodiversity benefits is optimal (Shogren et al. 1999; Naidoo et al. 2006). Cost-effectiveness of alternative conservation measures is a relevant aspect of any successful conservation strategy.

In this paper, we report a simulation analysis of how limited conservation resources could be cost-efficiently allocated for alternative conservation strategies. Notice that we do elicit the optimal strategy for the society including all social costs, because full social costs of alternative conservation strategies are unknown. Instead, we opted for a value-for-money approach for a given conservation budget assuming that the resources allocated for conservation reflect social costs and benefits. We compare a status quo scenario, which reflects the current intensive timber-centered forest management in Fennoscandia with four alternative scenarios. In each of the four alternative scenarios, a fixed amount of funding is assigned for temporary or permanent reserves to enhance conservation of biodiversity in a landscape. We simulate forest growth and succession at forest stand level over 100 years to project and compare the scenario outcomes in time.

For effective biodiversity management, it is critical to know what habitats will maintain particular species or species groups in alternative management strategies (see e.g. Wikberg et al. 2009). Conservation efforts should be directed to focal species that are vulnerable to human-induced landscape changes, e.g., red-listed species. However, there is considerable variation in habitat requirements of red-listed forest species (e.g. Tikkanen et al. 2006). Thus, any single scenario may not efficiently conserve all species, but the conservation value of the scenarios may differ depending on the focal species.

In boreal and hemiboreal forests, a large fraction of species are associated with dead and decaying wood. In Fennoscandia, 20–25% of forest-dwelling are dependent on dead-wood habitats (Siitonen 2001). Species dependent on dead-wood constitute 60% of red-listed species of boreal forests in Fennoscandia. Among boreal tree species, Norway spruce (*Picea abies*) hosts the greatest number of red-listed species (Jonsson et al. 2005; Tikkanen et al. 2006). Therefore, we opted to measure biodiversity benefits by estimating the amount of coarse woody debris (CWD) originating from Norway spruce in the alternative scenarios. We also assessed forest stand quality using habitat suitability modeling approach (see Tikkanen et al. 2007) for red-listed species dependent on dead spruce logs. Habitat suitability for each species was based on its habitat requirements regarding tree species, size class of trees, stage of decay, and tolerance to sun exposure.

Materials and methods

Study area

Our study area is located in central Finland (62° 14′ N, 25° 45′ E). It is a typical forest landscape for the region with scattered bogs, lakes, and cultivated areas. The land is mostly privately owned and average size of a holding is 24 ha (Finnish Forest Research Institute 2008). The area was 10,000 ha of which 71% was covered by forest land. The most common forest types in the region are the mesic spruce-dominated forests (Myrtillus type, MT; for classification, see Cajander 1949)), subxeric pine-spruce forests (Vaccinium type, VT), and herb-rich mixed spruce-deciduous forests (Oxalis-Myrtillus type, OMT) covering 43, 27, and 20% of the forest land, respectively.

We derive landscape data from National Land Survey of Finland (soil data) and Finnish Environment Institute (land cover types). We reclassified these data into settlement and roads, fields, forest land on mineral soils, peatland, and lakes. We used 10-m resolution in raster data.

Simulations

We began simulations by setting all landscape characteristics that remained static throughout the simulation (soil

properties, land cover types, forest types, stand sizes, and initial stand ages) using regional information (Finnish Forest Research Institute 2008). We randomly allocated forest stands of each forest type on mineral soils. We generated forest types in landscape in the order of their abundance starting from the rarest one. We picked the size for each forest stand from a normal distribution (mean 2 ha and standard deviation 1 ha). We assigned the initial stand age to each stand according to prevailing forest age distribution in the region (mean 51 years and standard deviation 37).

Our analysis is based on a hypothetical landscape because we did not have access to forestry files concerning privately owned forests in the region. However, our data with the variation in the stand characteristics emulate the existing variation among spruce forests in our study region. In this work, we focused on mesic spruce-dominated (MT) and herb-rich mixed spruce-deciduous (OMT) forest types because species-habitat data are presently the most comprehensive for these types. For MT- and OMT-forest stands, we additionally attributed stand history. Ninety percent of MT and OMT stands had been managed according to the current management recommendation (including soil preparation and planting of new trees on clear-cuts, sapling treatments, 1–2 thinnings before final clear-cut harvesting with a mean rotation period of 70–90 years; Tapio 2006). On the remaining 10% of the stands, present official management recommendations had been ignored. To emulate existing variation in stand composition, we varied the proportion of spruce in stands. Initially, 25% of stands had 15% spruce, 50% of stands had 45% spruce, and the rest had 75% spruce of the total timber volume.

Subsequently, we placed nature reserves in the landscape reflecting their present cover and size variation in the region. At the start, simulated landscapes contained one larger nature reserve (71 ha) and 35 smaller protected areas (woodland key habitats, see Timonen et al. 2010) representing a typical situation in the region. We randomly located the nature reserve on the simulated forest land and set its size to 1% of the total forest land area. Because we assumed this nature reserve had been established in the past, we increased the age of all stands within the reserve by 40 years. We assigned woodland key habitats to forest stands ≥80 years old in the managed landscape. We randomly picked their size from a log-normal distribution (mean 0.58 ha and std 0.77) following Kotiaho and Selonen (2006). Thus, they covered 20 ha (0.3% of total forest land) in all simulations.

In simulations, we processed changes to the initial state via subroutines at 5-year time steps over 100-year period. We updated successional state at each step by first increasing the stand age by 5 years, and then updating the attributes for a given forest type, harvest history, and proportion of spruce over the stand. We included no disturbances other than forest management in the simulation because we aimed at comparing the effects of alternative forest management practices. Furthermore, efficient fire suppression in Finland has practically eliminated fires from the country. We updated a raster storing the edge effect at each time step. We defined an edge effect as changes in microclimatic conditions resulting from a 30-m (three raster cells) band along a stand border if it faced another forest stand less than 20 years of age or a non-forested land cover type. After updating succession, we processed habitat suitability index (HSI) for the species by extracting parameters from rasters and text files, and calculating HSI equations anew for each MT- and OMT-forest stand (see below).

We generated forest growth, yield tables, and dead-wood data using MOTTI stand simulator (Hynynen et al. 2005). We obtained the volume of fresh CWD from MOTTI simulation results in each 5-year period (CWD cohorts), and, using equations of Mäkinen et al. (2006), we calculated change of volume and density of each CWD cohort and updated the simulations. We used density of CWD as indicator of decay stage. We regarded a CWD cohort as fully decomposed and removed it from calculations when its density was <15% of original density (Tarasov and Birdsey, 2001). When density of CWD was between 15 and 30% of the original density, we set decay stage to 5 (wood very soft and breaks easily in parts). Density between 30 and 55% corresponded to decay stage 4 (no bark, wood soft), between 55 and 75% to decay stage 3 (bark loose and partially fragmented, surface wood soft) and >75% to decay stages 1–2 (bark intact, wood material hard) (see Tikkanen and Kouki 2007, for details).

We allowed no harvesting in permanent nature reserves or woodland key habitats. Otherwise, five percent of forest area was harvested (stand age set to zero) at each 5-year time step (corresponding to 100 years harvest rotation). We randomly selected stands to be harvested among stands with age ≥65 years.

Scenarios

We explored four scenarios to conserve and maintain habitat for forest-living dead-wood dependent species. We compared the simulated effects of these management scenarios with the current (status quo) forestry practices. We used the budget figures used in the preparation and implementation of the recently introduced national METSO II forest conservation program (Ministry of the Environment 2008) to cost out our scenarios and to assure applicability of our results. All scenarios except status quo were limited by the same fixed conservation budget for biodiversity conservation. A total of 182 million € for additional conservation efforts in southern Finland were allocated through METSO II during 2008–2012. Assuming

that this effort will be evenly spread across southern Finland and that equal effort will be allocated also for the whole 100-year simulation period, c. 85,000 € would be available for conservation in each 5-year period on our 10,000 ha study landscape.

Following the report of the METSO II program working group, we used purchase price of 4800 €/ha for land acquisition (Ministry of the Environment 2008). We set land leasing costs at 1290 €/ha for 10-year contracts based on empirical data from a pilot project in SW Finland (Gustafsson 2007). Thus, the conservation budget allowed purchase of 18 ha of forest for protection during each 5-year period. Alternatively, the budget could be allocated to establishing new temporary land leases of 67 ha during the first two periods. After 10 years, budget could be allocated to renew old contracts or purchase of new sites.

We ran each scenario four times. In each simulation, we created the initial spatial state of the landscape anew, and thus, the replicates can be considered independent. We compared the following scenarios:

(1) *Status quo*. This represents the current situation. No additional resources were allocated to conservation, and biodiversity gains reflect the balance between natural forest growth and management pressure that is assumed to remain at a similar level throughout the simulation period.
(2) *Permanent large reserves* (*PLR*). All available funds were allocated to purchase of 356 ha of forest to establish new large reserves at the beginning of the simulation. The scenario used five blocks of reserves: one old reserve (71 ha) and four new ones (each 89 ha). The new reserves were located in a landscape so that new reserves predominantly resided in forest stands where management recommendations had been ignored.
(3) *Temporary small reserve* (*TSR*). New reserves were leased and protected for periods of 10 years. Budget permitted establishment of 67 ha temporary reserves during the first and second 5-year time steps. Subsequently, the total area in small temporary reserves was held constant at 134 ha using the following three steps: locate potential sites, renew a contract with probability of 0.5 or otherwise cancel it, and establish new contracts.
(4) *Permanent small reserves* (*PSR*). In the permanent small reserve scenario, new reserves were established 18 ha per 5 years. The potential new TSR and PSR sites were ranked based on the HSI-value of the forest stand. New reserves were accepted in the order of their rank. The sizes of small reserves were randomly picked from a log-normal distribution (mean 3.5 ha and std 2.4 ha) derived from statistics of real transactions (Gustafsson 2007).
(5) *Green-tree retention (GTR)*. During each 5-year time step, 18 ha were allocated as tiny (10 × 10 m) set-asides (retention trees or tree groups) on stands that were clear-cut. The number of pixels left unharvested per stand was proportional to the stand size (on average 5% of stand area).

With a fixed conservation budget, scenarios differed in how protected forests area cumulated in time. In status quo scenario, protected area remained at 1.3% of the total forest area throughout the 100-year simulation. In the PLR scenario, all funding was immediately allocated to four additional permanent reserves of 356 ha in total covering about 6.1% of the total forest area. In the PSR and the GTR scenarios, 18 ha increment per each 5-year period resulted in steady increase of protected area. Similarly, in the TSR scenario, conservation budget was even in time. This resulted in relatively rapid increase in the amount of protected forests because it is possible to acquire more land temporally via leasing than permanently via purchase. However, after 20 years, all funding was tied to renewal of the existing contracts or renting new sites to substitute the ones for which contracts terminated. After 20 years, the area of protected forests remained at the fixed level of 220 ha (3.1% of the total forest area). After a 100-year period, all other scenarios included roughly the same area of protected forests except the status quo and the TSR.

Species data and HSI functions

We estimated the effects of different management scenarios on habitats of red-listed (Rassi et al. 2001) dead-wood dependent species using habitat suitability indices (HSI; Tikkanen et al. 2007) for 25 species dependent on dead spruce in southern Finland. We obtained habitat requirements for these species from Tikkanen et al. (2006). We classified species into five groups with similar requirements within a group (Table 1).

The first species group labeled Monuru after the type species, *Monochamus urussovii,* includes two species associated with fresh spruce dead-wood in decay stage 1 and 2. This species group has no other habitat requirements (Table 1), and the HSI is determined only by one sub-priority function (R_1 in Table 2). The second species group, Trilar (*Trichaptum laricinum,* 3 spp.), is associated with dead-wood in late decay stages (3 and 4) but has no further requirements. The species groups Araero (*Aradus erosus*, 3 spp.) and Skebre (*Skeletocutis brevispora*, 15 spp) require dead spruce trees, either fresh or well-decayed, in shade. Thus, their HSI is a function of two sub-priorities. Finally, the fifth group (Acmmar, *Acmaeops marginata*, 2 spp.) requires fresh, large diameter dead-wood in sun-exposed sites, and HSI is determined by three sub-priorities.

Table 1 Ecological characteristics of the five species groups of the study and their HSI functions

Species group	Species *n*	Preferred decay stage		Prefer large logs	Microclimatic requirement[a]		HSI functions
		1 & 2	3 & 4		Shade	Sun	
Monochamus urussovii	2	X					R_1
Trichaptum laricinum	3		X				R_2
Aradus erosus	3	X			X		$(R_1*M_1)^{1/2}$
Skeletocutis brevispora	15		X		X		$(R_2*M_1)^{1/2}$
Acmaeops marginata	2	X		X		X	$(R_1*D*M_2)^{1/3}$

[a] Effect of edge on HSI: *shade* negative, *sun* positive

Table 2 Sub-priority functions used in habitat suitability indices of red-listed spruce species

Sub-priority	Function
R_1	$= 1.454\,\frac{Q_{pds}}{26.122+Q_{pds}}$
R_2	$= 1.130\,\frac{Q_{pds}}{5.619+Q_{pds}}$
D	$= -0.006 + \frac{1.014}{\left[1+\exp-\left(\frac{d-13.621}{2.397}\right)\right]5.056}$
M_1	$= 0.15 * BA^{0.5}$
M_2	$= -0.07 * BA^{0.5} + 1$

Values of sub-priority functions were scaled between 0 and 1

R quantity of dead-wood, *D* diameter, *M* microclimate, Q_{pds} quantity of dead-wood in preferred decay stage, *d* mean diameter of preferred dead-wood, *BA* basal area of stand

We calculated HSI-values as the geometric mean of sub-priority models (Tikkanen et al. 2007). We scaled the dead-wood component of HSI sub-priority models using results from empirical studies from Finnish spruce forests (Martikainen et al. 2000; Penttilä et al. 2004). At the stand level, a total amount of 80 $m^3\ ha^{-1}$ of dead-wood is sufficient even for the most demanding species (Tikkanen and Kouki 2007). Moreover, we assumed that in old-growth spruce forest ecosystems, the input and output of dead-wood is constant. Using decay models from Mäkinen et al. (2006) and definitions of different decay stages given in Tikkanen and Kouki (2007), we calculated proportions of different decay stages from total amount of dead-wood composed of successive cohorts of dead logs of equal size. We adjusted the sub-priority value for the amount of preferred type of dead-wood between 0 and 1, 1 representing the optimal condition. We fitted a convex curve $R_n = a\frac{Q_{pds}}{b+Q_{pds}}$ for this sub-priority where Q_{pds} is the volume of dead-wood in preferred decay stage with which the species group is associated, and *a* and *b* are constants (Table 2).

Some dead-wood dependent old-growth species are known to be associated with large diameter dead-wood. For these species, we created a second sub-priority model based simply on diameter of dead spruces. Diameter of 30 cm is commonly used as the limit for large logs in Fennoscandia (Tikkanen et al. 2006). However, this limit is not strict, and these demanding species can sometimes occur also on smaller logs. In this sub-priority, we used a sigmoid function

$$D = D_0 + \frac{a}{\left[1+\exp-\left(\frac{d-d_0}{b}\right)\right]c}$$

where *d* is mean diameter of preferred type of dead-wood and *a*, *b*, *c*, D_0, and d_0 are constants in the equation. *D* achieved maximum value of 1 at diameter of 30 cm (Table 2).

The microclimatic requirements of red-listed forest species are highly variable; some species being dependent on moist and shady old-growth conditions, some species preferring sunny sites, and some species seeming to be indifferent to variation in microclimate (e.g. Berg et al. 1994; Tikkanen et al. 2006). Inside a forest stand, microclimatic conditions are largely determined by the solar radiation penetrating canopy. Basal area of a forest stand and canopy cover are tightly linked, and we used this relationship in the sub-priority models describing microclimatic requirements of species. Sub-priority for microclimate was $M = a * BA^{0.5} + b$, where *BA* is basal area of stand and *a* and *b* are constants. For species dependent on shade and moist microclimate, the relationship between basal area and habitat quality was positive, but negative for species preferring sunny sites (Table 2).

We incorporated edge effects into the microclimate sub-priority function by multiplying the HSI by (1 − edge-ratio) for species requiring shade and by (1 + edge-ratio) for species group requiring sun-exposed sites. Edge-ratio is the proportion of stand area within 30 m from the nearest edge to recently (<20 years) clear-cut forest or permanent open area (field, open peatland, lake, etc.). For species requiring sun-exposed sites, we rescaled HSI * edge-ratio to vary between zero and one.

Analyses

We first estimated biodiversity benefits in each scenario by the area of forests containing more than 20 m^3/ha of CWD. We chose the 20 m^3/ha CWD volume threshold because earlier studies have shown that red-listed species tend to appear in a forest stand only above this volume threshold

(Martikainen et al. 2000; Penttilä et al. 2004). We further compared alternative scenarios by calculating the sum of HSI-values across species groups and across all MT- and OMT-forest stands in the study area. We also calculated the area (ha) of forests where HSI-value was ≥0.8, i.e. highest quality stands for the species group, to assess habitat availability.

We present the results for the alternative scenarios relative to those from the status quo scenario, i.e., numbers from simulation were divided by mean value from the corresponding status quo scenario. Thus, we compared alternative scenarios with each other relative to the status quo. All spatial modeling was carried out with the Spatially Explicit Landscape Event Simulator (SELES; Fall and Fall 2001).

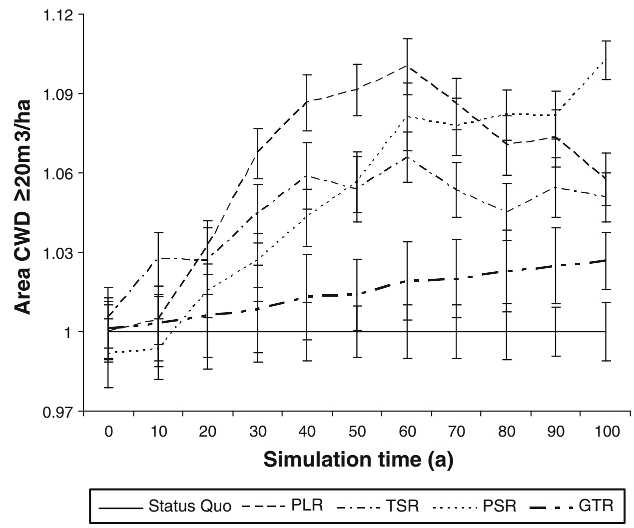

Fig. 1 Trajectories in time for the area of dead-wood rich forests (CWD >20 m^3/ha) in different scenarios. Y-axis is scaled to status quo scenario at each time step. *Error bars* represent ±1 SE

Results

The amount of timber harvested did not considerably differ among the scenarios. In the status quo scenario, an average of 103,100 m^3 (SE across 4 simulations 4,350 m^3) of timber was extracted per each 5-year period of simulation. For the PLR scenario with the lowest timber yields, the corresponding value was 102,850 m^3 (SE = 4,179 m^3), a difference of 0.24%.

Scenarios differed in terms of the area of dead-wood rich (≥20 m^3/ha of CWD) forest (Fig. 1). In the status quo scenario, the area of dead-wood rich forest averaged 750 ha (±18 SE) across the 100-year simulation period. The PLR and GTR scenarios provided, respectively the greatest (6%) and lowest (1.5%) increases in the area of dead-wood rich forests among the alternative scenarios. In the short term (10 years), the TSR scenario yielded the greatest increase in area of dead-wood rich forests. The PLR scenario performed best at intermediate time intervals (40–60 years) while PSR was the most effective in the long run (90–100 years; Fig. 2). Over the 100-year simulation period, the highest absolute area (940 ± 15 ha) of dead-wood rich forest was attained under the PSR scenario. This was 10% more than in the status quo scenario and 4% more than in the PLR scenario.

There were considerable differences in the rate of increase and in the relative HSI gain among scenarios and species groups. Species that were indifferent with respect to microclimate and required mainly recently dead-wood (Monuru) showed a rather quick positive response to conservation effort under all alternative scenarios except GTR. After only 10 years, the PLR, PSR, and TSR scenarios differed from the status quo scenario in terms of HSI (Fig. 2a), and after 40 years, the PLR and PSR scenarios clearly outperformed all others and yielded c. 25% higher HSI-sums than the status quo scenario.

Species requiring later decay stages but being indifferent to microclimate (Trilar) responded to additional conservation effort, but differed from the status quo scenario only after 20–30 years (Fig. 2b). For this species group, the GTR scenario also had slightly higher HSI-sums (c. 3%) than did the status quo scenario. The other three scenarios, however, clearly performed better yielding on average 10% (TSR), 19% (PSR), or 29% (PLR) higher values than the status quo scenario. The difference relative to the status quo increased with time, and after 100 years, the HSI-sum was 31% and 54% higher in the PSR and PLR scenarios, respectively.

Species residing on recently dead-wood but requiring shade (Araero) also responded to additional conservation effort with time lags (Fig. 2c). HSI-sums for the GTR and TSR scenarios did not differ from those for the status quo scenario, but the PLR and PSR scenarios outperformed other scenarios after 30 years. Overall, these latter two scenarios yielded about 17% higher HSI-sums than did the status quo scenario.

Species requiring later decay stages and shade (Skebre; Fig. 2d) fared best in the PLR scenario, under which the HSI-sums attained higher values than in the status quo scenario. On average, these were 15 and 28% higher, respectively, after 30 and 100 years of simulation. The PSR and TSR scenarios did not differ, both providing on average 6% higher HSI-sums than the status quo. The GTR scenario clearly performed worst, yielding on average 7% lower HSI-sums than the status quo.

Species associated with recently dead-wood and benefiting from sun exposure (Acmmar) showed only subtle differences among scenarios in the relative HSI-sums

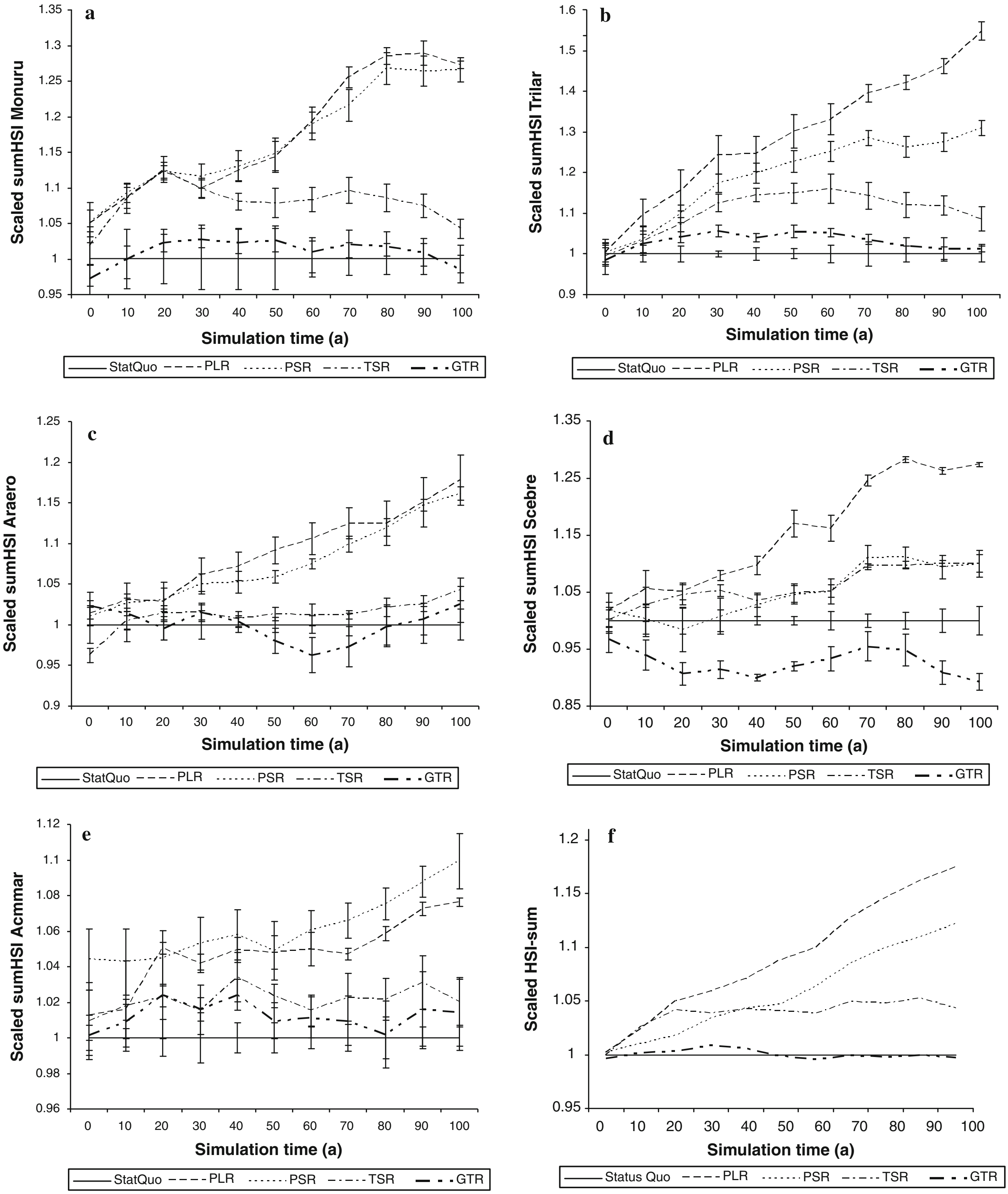

Fig. 2 Trajectories of HSI-sum over all stands in the landscape for different species groups (**a**–**e**) and for all species groups combined (**f**). Y-axis is scaled to status quo scenario at each time step. *Error bars* represent ±1 SE

(Fig. 2e). Even though the HSI-sums tended to be highest in both the PSR and PLR scenarios, difference from the status quo scenario averaged only about 5% across the 100-year simulation. The use of PSR tended to outperform other scenarios, particularly toward the end of the simulations. The other two alternative scenarios (TSR and GTR)

yielded only slightly higher HSI-sum values (by about 1–2%) than the status quo scenario.

We pooled all species groups and calculated the sum of average HSI-sums across all species groups. HSI-sum trajectories in time (Fig. 2f) in the TSR and PSR scenarios followed the pattern in the increment in protected area (see "Methods"), i.e. monotonic increase for PSR, and first increase then plateau for TSR. The PLR scenario also showed a monotonic increase in the total HSI-sum and reached higher values than the other scenarios particularly in the end of the simulation. When calculated across all species, GTR scenario provided no biodiversity benefits relative to the status quo.

When only the high-quality stands (HSI $\geq$ 0.8) were considered, there were considerable differences in the relative effectiveness among alternative scenarios (Fig. 3). The PLR and PSR scenarios tended to provide the highest habitat availability, up to three or four times more high-quality sites than did the status quo scenario. The TSR scenario provided a notable relative increase in HSI, particularly in the short term, for species having only one sub-priority function (Fig 3a, b), but did not differ much from the status quo for species requiring fresh dead-wood and shade (Fig. 3c). The GTR scenario seemed only to benefit species that require fresh dead-wood in sun-exposed sites (Fig. 3e).

For species requiring old dead-wood and shade (Fig. 3d), temporal patterns of high-quality habitat availability were rather irregular, reflecting mainly low habitat availability and the consequent action of chance in all scenarios for this species group. The average amount of high-quality forest for these species in the status quo scenario across 100-year simulation period was 0.1% of the total area of MT and OMT forests (i.e., 5 ha); in the PLR scenario, the average was 0.3% (14 ha).

The highest levels of habitat availability were predicted for species requiring fresh dead-wood in sun-exposed sites. For example, the average value in the status quo scenario was 2.7% of the total area of MT and OMT forests (120 ha) when compared with 3.5% (155 ha) under the PSR scenario. Thus, for this species group, the relative benefits of alternative conservation measures were much lower than for other species groups, with a maximum of 46% increment in the area of high-quality stands compared with the status quo (PSR in the end of the simulation; Fig. 3e).

Discussion

Biodiversity gains from additional conservation efforts depend mainly on how the benefits are measured and the time frame these benefits materialize on a managed forest landscape. We measured these in terms of habitat suitability for five groups of species associated with decaying Norway spruce. The area of dead-wood rich forests (Fig. 1) tended to correlate with increases in the area of protected forests. Likewise, the overall habitat quality of the landscape, when measured as HSI-sums, increased proportionately to the increase in the area of protected forests for species having the least restrictive habitat requirements (Fig. 2a, b). The monotonic increase in HSI-sums for these species and also across all species groups in the PLR scenario (Fig. 2f) suggests that time lags should be expected with respect to results from such conservation efforts.

The relative effectiveness of alternative scenarios depended on the time frame over which the benefits were measured. Short-term gain in the area of dead-wood rich forests was highest in the TSR scenario, but the PLR and PSR scenarios provided the most increase over intermediate and long-term time frames, respectively (Fig. 1). In many aspects, temporary conservation (TSR) was as effective as permanent conservation (PLR and PSR) for the first 20–30 years, but this measure did not produce as much habitat as did permanent conservation in the long run.

The response of species groups varied according to their habitat requirements. For species whose preferred habitat was common (Fig. 3e), there were no ecologically meaningful differences among scenarios. Habitat availability for these species measured as area of forest with HSI $>$ 0.8 in different scenarios increased by less than one percent over the status quo scenario. For these species, there was much habitat available in the landscape at all times, and thus, conservation gains were minor. More demanding species that require rare habitats ($<$2% of forest area) showed stronger responses to additional conservation efforts. For the most demanding species, the budget was not large enough to enhance habitat availability in any scenario (Fig. 3d), and in all scenarios, the proportion of high-quality stands remained at $\leq$0.3% of the total forest area.

The availability of habitat for dead-wood associated species was affected by forest edge in the simulation. For species avoiding forest edges (requiring shade), the PLR scenario clearly provided the largest area of habitat (Fig. 3c, d). Edge habitat is pervasive in managed forest landscapes, and the more small sites are protected the more such sites face intensively harvested areas, lowering their quality for edge-sensitive species. Therefore, there was a constant scarcity of habitat for edge-sensitive species at all times because of annual clear-cuts. Basically, all additional conservation effort, especially under the GTR scenario, was affected by the edge effect (Fig. 3c, d). However, even for species preferring edge, the GTR scenario did not provide larger landscape-level benefits than the other scenarios (Figs. 2e, 3e). This is because in boreal landscapes, natural forest edges abound even in large permanent reserves.

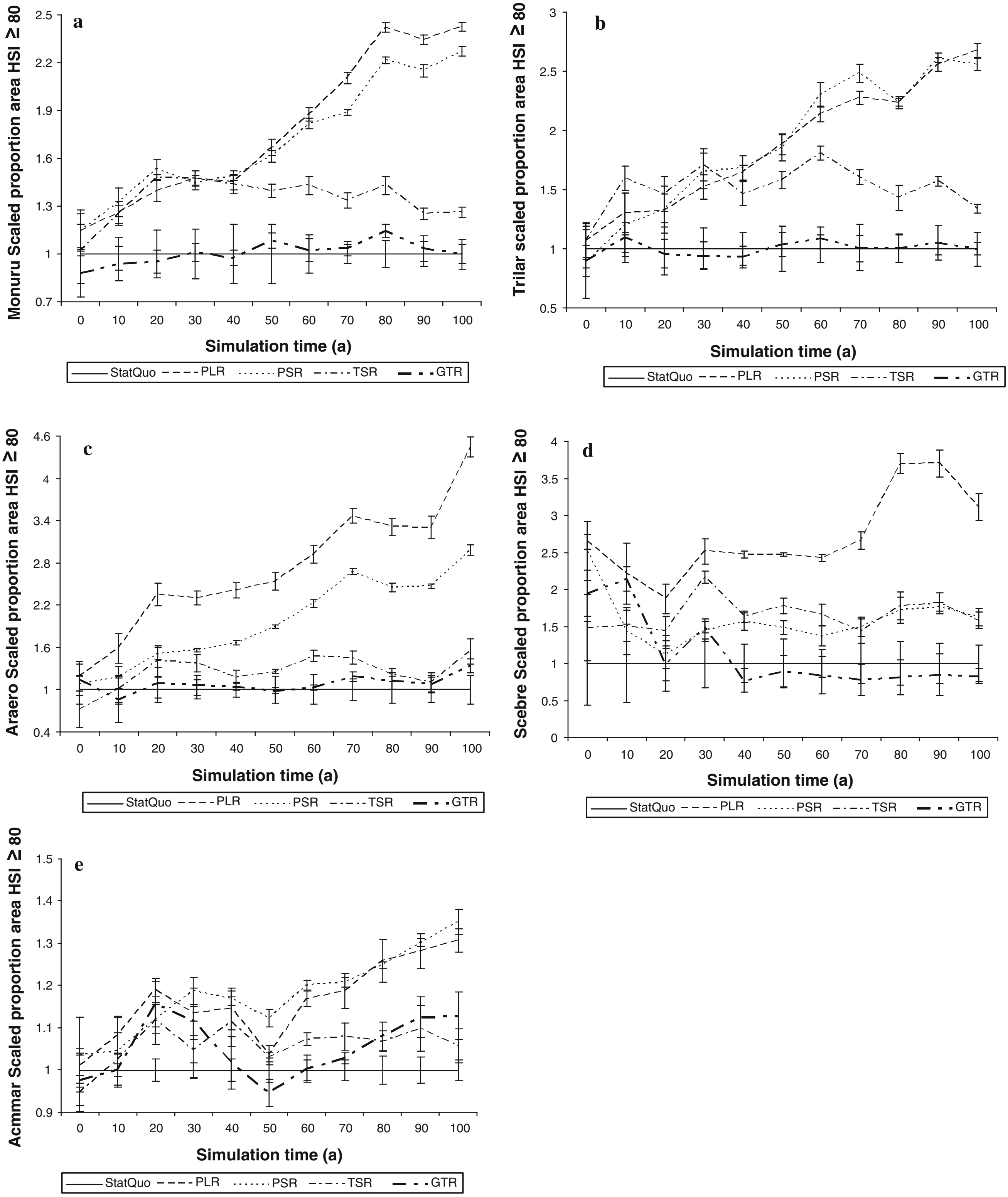

Fig. 3 Trajectories of forest area over all stands in the landscape where HSI-sum >0.8 for different species groups (**a**–**e**). Y-axis is scaled to status quo scenario at each time step. *Error bars* represent ±1 SE

PLR scenario resulted in the best overall landscape quality for most species groups. Large reserves were diverse in habitat types and age classes, but some forest attributes, such as the amount of dead-wood (Fig. 1), began to decline with time in aging forests after 60 years of simulation. Large reserves also minimized local edge effects. However, when

established on land with intensive forestry history rather long time delays are required to realize biodiversity benefits.

A strategy of using PSRs potentially discovers and protects dead-wood rich sites efficiently and area protected increases constantly, but not as rapidly as in TSR. Consequently, the PSR scenario produced long-term biodiversity benefits for dead-wood dependent species nearly equivalent to the PLR scenario. Permanent small sites were very sensitive to edge effect caused by management of the neighboring stands, and therefore, their long-term conservation value depended on both predictable processes that gradually alter inherent forest attributes and somewhat unpredictable external factors such as harvesting in the near-by forest stands.

The TSR scenario provided faster increases in protected area in the short term than the use of PSRs because it is possible to acquire more land temporally via leasing than permanently via purchase. The long-term costs and hence relative utility of land leasing versus purchasing depend on e.g. interest rate, and for the prices, we used here it is less expensive to purchase than to lease land for conservation if the interest rate is less than 3% (see Juutinen et al. 2008). We assumed that new TSRs will include the highest quality sites, which may not be an overly optimistic assumption (Mönkkönen et al. 2009). In TSR scenario, both the area of dead-wood rich forests (Fig. 1) and the habitat availability for some species groups (Fig. 3a, b) first increased rather rapidly and then leveled-off, reflecting the pattern in the overall area under protection. The possibility of spatial changes of TSRs results in a dynamic site network, which may not be the most efficient use of limited resources. For example, habitat for species requiring well-decayed dead-wood diminished over time in the simulations (e.g., Figs. 2b, 3b, d). Temporary land leases, such as in our TSR scenario, may be a useful method because it resulted in the most rapid improvement in landscape quality. Conservation of ephemeral forest attributes (e.g. postfire succession and associated highly dispersive species) matches best with this conservation strategy (Mönkkönen et al. 2009).

The GTR scenario seemed not to increase habitat availability for any species group and is thus an ineffective use of conservation funding. Similarly, Djupström et al. (2008) found that retention tree groups on clear-cuts tend to contain less dead-wood and to host fewer species than larger set-asides. Our models on the dead-wood dynamics in the GTR patches may miss some important aspects. For example, it has recently been shown that the amount of CWD may be higher in GTR patches than in comparable mature forests, probably because windstorms increase dead-wood formation in edge-prone GTR patches (Hautala and Vanha-Majamaa 2006; Jönsson et al. 2007). Thus, GTR may promote the distribution of key forest attributes in a landscape. It is, however, uncertain which species are supported and maintained by retention trees and tree groups (Rosenvald and Lõhmus 2008). GTR sites were by definition edge habitat for the first 20 years, and therefore, species avoiding forest edges do not survive in those sites.

Time frame is a seldom addressed aspect in planning of conservation policies. Our results suggest that biodiversity benefits of conservation efforts may become visible with a considerable time lag, and alternative scenarios differed in how fast they were able to increase landscape quality or augment species-habitat availability. Therefore, the choice of appropriate conservation policy depends on whether short- or long-term conservation gains are expected. In conclusion, we suggest that conservation programs should specify explicit goals and assess expected conservation gains over time in the process of selecting the most appropriate methods to achieve these goals. Short-term and long-term goals may well differ, and thus, conservation tools should be tailored to meet these changing goals in time.

Conservation budget is always a decision resulting from political bargaining. In this study, we used the budget level according to the METSO II program. Because HSI-values are deterministic and do not carry spatial information budget, the results from our simulation are linear within the realistic range of budgets: halving the budget would halve the ecological benefits. Non-linear patterns would be expected when spatial configuration of habitat becomes important (Mönkkönen and Reunanen 1999). Non-linear patterns in landscape quality and habitat availability may also appear when marginal benefits from conservation considerably decrease with increasing budget. This will only happen with larger than realistic budget levels, i.e. when habitat quality becomes a limiting factor.

We considered here the alternative scenarios as exclusive conservation policies. In reality, several methods can be applied simultaneously. It is very important from the practical perspective to know the most cost-efficient combination of methods. This combination may well vary according to conservation budget, conservation time frame, species group, and among regions depending on their land-use history and current landscape structure. Eliciting optimal combination of alternative methods is an important challenge for future research.

Acknowledgments Financial support from the Ministry of the Environment (YM34/065/2006) made this study possible. We thank A. Fall for assistance during the project. We are grateful to Panu Kuokkanen, Timo Lehesvirta, Antti Otsamo, and Juha Siitonen for comments on this work.

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